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Species richness change across spatial scales

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Species richness change across spatial scales

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Species richness change across spatial scales

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Abstract

Humans have elevated global extinction rates and thus lowered global-scale species richness. However, there is no *a priori* reason to expect that losses of global species richness should always, or even often, trickle down to losses of species richness at regional and local scales, even though this relationship is often assumed. Here, we show that scale can modulate our estimates of species richness change through time in the face of anthropogenic pressures, but not in a unidirectional way. Instead, the magnitude of species richness change through time can increase, decrease, reverse, or be unimodal across spatial scales. Using several case studies, we show different forms of scale-dependent richness change through time in the face of anthropogenic pressures. For example, Central American corals show a homogenization pattern, where small scale richness is largely unchanged through time, while larger scale richness change is highly negative. Alternatively, birds in North America showed a differentiation effect, where species richness was again largely unchanged through time at small scales, but was more positive at larger scales. Finally, we collated data from a heterogeneous set of studies of different taxa measured through time from sites ranging from small plots to entire continents, and found highly variable patterns that nevertheless imply complex scale-dependence in several taxa. In summary, understanding how biodiversity is changing in the Anthropocene requires an explicit recognition of the influence of spatial scale, and we conclude with some recommendations for how to better incorporate scale into our estimates of change.

Keywords: biodiversity, spatial scale, time, change, species richness, anthropogenic change

Introduction

Biodiversity is changing through time at a rapid pace, and anthropogenic factors such as land-use intensification and climate change are directly and indirectly responsible (e.g., Pereira et al. 2012, Pimm et al. 2014, Ceballos et al. 2015). Such biodiversity change has profound influence on the functioning and stability of natural ecosystems and the people who depend on them (e.g., Cardinale et al. 2012, Isbell et al. 2017), precipitating a number of international collaborations and policies to understand and manage these changes (e.g., Aichi targets of the United Nations' Convention on Biodiversity; Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES); e.g., Tittensor et al. 2014, Diaz et al. 2015). Exactly how this change is manifest, however, has been the subject of some debate. At the global scale, historical and modern anthropogenic factors have directly and indirectly caused the extinction of many taxa (Barnosky et al. 2011, Pimm et al. 2014, Alroy 2015, McCauley et al. 2015), leading to a decline in global-scale species richness. While it is sometimes assumed that global extinctions are reflected across all spatial scales, this is not always, or even often, the case. Instead, exactly how species richness changes at scales smaller than the globe is more nuanced and has been the subject of some debate (see e.g., Primack et al. 2018 for an overview).

Change in the numbers of species through time at scales smaller than the globe (i.e. in the absence of speciation), will depend on the balance between losses and gains of species from one point in time to the next (e.g., Sax et al. 2002, Jackson and Sax 2010, Blatt et al. 2017, Dornelas et al. 2019). In this article, we do not enter into the debate about whether fine-scale species richness is changing in the face of human activities (e.g., Vellend et al. 2013, Dornelas et al. 2014, Gonzalez et al. 2016, Cardinale et al. 2018), but rather simply acknowledge that the observed pattern of change is variable, with some intriguing biogeographic and taxonomic variation (Newbold et al. 2015, Blowes et al. 2018). Nor do we distinguish among types of

species involved in any change (e.g., native vs non-native, specialist vs generalist), even though turnover in species composition is more responsive to environmental change than species richness change (e.g., Supp and Ernest 2014, Dornelas et al. 2014, Hill et al. 2016, Hillebrand et al. 2018). Instead, our main purpose is to emphasize that species losses and gains though time are asymmetric across spatial scales. It only takes one individual of a new species to result in a gain, but requires the loss of all individuals of a species to lead to a loss. Given this asymmetry, it is likely that the magnitude of species richness change through time, and even its direction (i.e., losses observed at some scales and gains at other scales) will be strongly influenced by the spatial scale under investigation (Cassey et al 2006).

Rates of loss of species from a given area via extirpations can be lower or higher than the global rate, and can be highly non-linear across scales (Hughes et al. 2007, Keil et al. 2018). Gains are likewise highly scale-dependent and result from the recolonization of previously extirpated species (e.g., McAlpine et al. 2016), range expansions (via climate change and human modification of habitat) (e.g., Batt et al. 2017), and/or introductions of species into their non-native ranges (e.g., Sax et al. 2002). As a result, biodiversity change, and especially the change in species richness through time, can often be scale-dependent (e.g., Sax and Gaines 2003, Cassey et al. 2006, McGill et al. 2015, Vellend et al. 2017a).

There have been numerous case studies illustrating the critical role of scale for understanding species richness change (e.g., Hill and Hamer 2003, Dumbrell et al. 2008, Keil et al 2011, Carvalheiro et al 2013, Jarzyna and Jetz 2018, Chase et al. 2018). However, the incorporation of spatial scale in modulating species richness change through time in the context of anthropogenic pressure has not been well considered in previous meta-analyses (e.g., Vellend et al. 2013, Newbold et al. 2015, Dornelas et al. 2014, Blowes et al. 2018; but see Elahi et al. 2015), even though the spatial extent of studies included varies by orders of magnitude (Cardinale et al. 2018). Nor has spatial scale been incorporated into conservation and scenario

modelling in the context of biodiversity-policy initiatives (e.g., Isbell et al. 2017, Purvis et al. 2018). Furthermore, when spatial scale is considered, it is often implicitly assumed that species richness change varies with scale in a relatively straightforward way, so that change observed at one scale can be used to predict change at another scale. As we will argue below, this expectation can often prove to be incomplete or wrong.

In the context of species richness change in the face of human impact, scale-dependence has been most often discussed regarding changes in site-to-site species composition, known as β-diversity (Socolar et al. 2016). For example, biotic homogenization (McKinney and Lockwood 1999, Olden and Rooney 2006) leading to a reduction in β-diversity, could be one explanation for why smaller-scale patterns of species richness (i.e., α-diversity) may not change (or even increase) despite larger-scale (i.e., γ-diversity) extinctions via Whittaker's (1960) diversity partition, $\gamma=\alpha*\beta$. However, the opposite pattern, an increase in β-diversity through time leading to biotic differentiation, is increasingly recognized as a frequent result of human impact (Socolar et al. 2016). This can occur, for example, via increases in habitat heterogeneity (e.g., multiple types of land-use in a landscape), introductions of species that remain relatively localized, or the loss of common/shared species among locations (Winter et al. 2009, de Castro Solar et al. 2015, de Carvalho et al. 2016).

Because both biotic homogenization and differentiation may be common, the direction of scale-dependence of species richness change following human impacts will be variable. As we illustrate below, the magnitude of species richness change can increase with scale under biotic homogenization, but decrease with scale under biotic differentiation. Thus, simply including the scale of observation as a covariate in synthetic analyses of species richness change would only yield interpretable results if one of these processes (and thus directions of scale-dependence) predominates.

In what follows, we first discuss the theoretical expectations for how patterns of species richness change through time, particularly in response to human pressures, and critically illustrate how these depend on the spatial scale of observation. We show that scale alters our observations of species richness change in a more complex way than typically assumed. Next, we illustrate this nuance with a series of case studies that show disparate scale-dependent responses of species richness change. Finally, we compile data from a number of sources that measured change through time across multiple taxa and scales. In summary, we show that the seemingly simple question of how species richness is changing through time in the face of anthropogenic change is not only scale dependent, but that this scale-dependence itself is more complex than typically assumed, and will require a great deal more work explicitly detailing the influence of scale in order to fully understand and synthesize patterns.

Theoretical framework for the scale-dependence of biodiversity change

The null expectation in the absence of any strong environmental change is that there should be no net change in species richness through time (despite species turnover) as a result of balanced colonizations and extinctions (e.g., MacArthur and Wilson 1967, Brown et al. 2001). At the global scale, and across very long time periods, this stasis would also depend critically on speciation and extinction events, but we do not consider this further. A number of factors associated with human impacts can alter this null expectation, including shifts in local environmental conditions (e.g., land use, environmental change), and regional shifts in the size and composition of the species pool (e.g., via introductions or extirpations) (Brown et al. 2001, Jackson and Sax 2010).

We use two qualitatively distinct model scenarios to illustrate the following: (i) that scale-dependence in species richness change is typical. (ii) that the nature of scale-dependence in

species richness change depends critically on model structure and parameter values. Details of the two model structures are presented in Appendix 1.

In the first model scenario, the metacommunity is altered by some hypothetical change such as that due to human impacts, but has not returned to equilibrium when richness is measured following the change. Here, there was strong scale-dependence between the average change in species richness through time and the spatial scale of observation, but this was strongly dependent on the structure of dispersal among localities (Fig. 1A). When dispersal was relatively high (intermediate and global), we often observed a hump-shaped relationship between species richness change and scale (see also Cassey et al. 2006, which had a similar model structure). However, the position of this hump-shape (whether richness increased or decreased in total) depended critically on the rates of local extirpations. When dispersal was more localized, scale-dependence was weaker and tended to be unidirectional towards more negative effects at larger scales (Fig. 1A).

In the second set of simulations, we allowed communities to return to a quasi-equilibrium following the hypothetical change. Here, the direction of change and its scale dependence were quite different. First, when we assumed that only the carrying capacity of the local community was changed by the perturbation, there were only increases or declines in equilibrium species richness through time, but these changes were not strongly scale-dependent (Figure 1B). However, when species colonization rates were also altered, we observed strong scale-dependence in equilibrium species richness change (Figure 1B). When colonization rates were increased, local species richness increased, but this effect declined with scale (sometimes leading to decreases at the largest scales) as a result of biotic homogenization. Conversely, decreases in colonization rates tended to decrease local species richness, but the magnitude of this decreased with increasing spatial scale (sometimes leading to increases at the largest scale) as a result of biotic differentiation.

By no means are these modelling scenarios complete, but even within our brief presentation, it is easy to see the breadth of possibilities of how species richness can change, and how that change can be scale-dependent, following some environmental perturbation. Nevertheless, there are some important general caveats to the simple simulations we have shown here. First, we assumed that environmental conditions are identical throughout the metacommunity, and that this does not change through time (e.g. is not influenced by human activities). However, in reality the environmental changes that result from human interventions not only directly influence species colonizations and extinctions, but do so indirectly by altering habitat characteristics. This can either increase habitat heterogeneity (more likely leading to differentiation) or decrease habitat heterogeneity (more likely leading to homogenization), which would alter the expected magnitude and direction of scale-dependent species richness change (e.g., Socolar et al. 2016). In addition, species in our models have no trait differences, whereas environmental changes such as those caused by human-modified landscapes are often associated with losses of narrowly distributed specialist species and gains in widely distributed generalist species, which could tip the balance towards biotic homogenization and greater losses at larger scales (e.g., Mckinney and Lockwood 1999, Eskildsen et al. 2015, Gossner et al. 2016). Such complexities would provide valuable information about the nuance in these relationships expected for specific real-world cases. However, fitting any of the model predictions to specific cases is beyond what we hope to accomplish here.

Recognizing that the modelling scenarios we presented in Figure 1 represent only a small fraction of the possibilities for how human activities can alter patterns of species richness and its scaling, we provide a more generalized framework that is necessarily more phenomenological in Box 1 (similar to, but more general than that presented by Chase et al. 2018). Specifically, we draw hypothetical Species-Area Relationships (SARs) for a given system, comparing between two time periods (before and after some hypothetical environmental or human-caused change).

By comparing the difference between the two SARs at any given scale, we can quickly see (i) how scale-dependence can emerge depending on how the parameters of the SAR change between time periods, and (ii) that the direction of scale-dependence will critically depend on the nature in which SARs are influenced.

Case studies illustrating scale-dependence of biodiversity change over time

We next illustrate case studies where patterns of scale-dependence were consistent with several of the hypothetical scenarios discussed above. While lacking generality, these case studies have the strength that the data are consistently gathered and directly comparable across nested scales across at least two time periods. Such nested observations collected with uniform methods is critical for quantifying true scale-dependent species richness change, but is only available for a limited number of case studies. For each system, we compared species richness from two time periods. Then we examined how species richness changed through time at different spatial grains (sampling points or geographic units) nested within that larger extent.

An overview of the case studies is provided in Table 1. Two of these case studies—corals near Central America and North American breeding birds—are based on surveys done at local scales to evaluate species richness change over a period of years to decades. The other two case studies—passerine birds from the Hawaiian archipelago and European plants—are based on checklists of species from smaller regions (e.g., islands, countries) that were nested to create checklists for the encompassing regions to evaluate scale-dependent changes due to human activities over centuries. In each case, we had information on species composition in addition to numbers of species present, gained and/or lost, and so we could nest the data at different spatial scales. For each case study, we plot the patterns and used quadratic ordinary

least squares regression with 10 and 90% quantiles for visualization (in Appendix 2, we provide some discussion of more formal statistical analyses).

Central American Corals—Reef-forming scleractinian corals were sampled across multiple reefs along the Pacific coast of Panama annually (full data and analyses presented in Gomez et al. 2018). In Figure 2A, we present data from multiple reefs over a 5-year period (2005-2009) where significant change in water temperature anomalies led to variable change in coral abundance and evenness. Nested sampling was organized as follows: (1) several one m^2 permanent quadrats were the smallest unit, and these were censused visually each year; (2) ten of these quadrats were along 10 m transects; (3) three transects (=30 quadrats) were in the upper slope of a reef and three transects (=30 quadrats) were in the lower slope of a reef; (4) the six transects from a reef were combined (=60 quadrats) to achieve a 'reef-scale' estimate; (5) five reefs (=300 quadrats) were censused in the gulf of Chiriqui and six reefs (=360 quadrats) were censused in the gulf of Panama to achieve 'gulf-scale' estimates; (6) all quadrats from all 11 reefs (=660 quadrats) were combined for the largest scale estimate (see Gomez et al. (2018) for further sampling methods and other details).

When we analyzed change in coral species richness over a five-year period, we found a scale-dependent effect (Figure 2A). At the smallest scales (quadrats, transects and reefs) some sites gained species while others lost species, but on average, there was no net change in species richness (regression quantiles overlap with zero). However, at the largest scales (entire survey), there was a trend for more species losses than gains (quantiles having no overlap with zero net change). This pattern is expected from the classic 'homogenization' scenario discussed in Box 1. Indeed, while local scale gains and losses were generally equalized, at the scale of the entire survey, more narrowly distributed species such as *Pavona frondifera* and *Pavona gigantea* were more likely to disappear from the surveyed quadrats, while widespread species such as *Pocillopora damicornis* and *Pavona clavus* became even more widespread.

North American Breeding Birds—Terrestrial birds were sampled annually from routes (~40.23 km with point counts every 0.8 km) spread across the United States and Canada as part of the North American Breeding Bird Survey (BBS) (for details, see Sauer et al. 2017). For this analysis, we used routes over a span of 30 years (1982-2011) that met quality tests in each of these years, resulting in a total of 393 routes (we did not use older data because the number of quality routes drops quickly). We binned the data into six 5-year periods to minimize noise and detectability issues. In order to nest surveys, we used routes in a rectangular area found between 95ºW to 70ºW and 30ºN to 50ºN. To nest areas, we subdivided the area into squares of 1º, 2º, 4º, 8º, 16º and the entire 25º x 20º area. For each grid cell size, we examined how many routes were found in each cell, choose an appropriate rarefaction level (capturing most but not all cells) and then used sample-based rarefaction so that all cells included in the analysis were sampled equally. Specifically, we rarefied to 1, 3, 6, 32, 150 and 393 routes for the 1º, 2º, 4º, 8º, 16º and full region grid sizes. The area shown on the x-axis in Figure 3B is based on the total directly sampled area rather than the size of the grid cells using 14.14 km^2 per BBS route (circles of 300 m radius at 50 point counts along each route). We fit trend lines over the six time periods and recorded the slopes to generate estimates of yearly species richness change within a transect.

In the BBS, we found a pattern opposite to that observed in the corals (Figure 2B). Rather than homogenization, we find a pattern more consistent with the idea of compositional differentiation through time in Box 1. Specifically, at the smaller spatial scales, there is again a considerable amount of variation whereby some sites have gains and others have losses in species richness, but overall no net change (regression quantiles overlap with zero). This result is largely consistent with the results of Schipper et al. (2016), who also found many sites with increases and decreases when they analyzed BBS data at this scale, but detected a slight increase in

species richness overall (use of different subsets of the data in both space and time could explain this discrepancy). However, when we nested data at larger spatial scales, we find a stronger and more consistent pattern of species richness increase over the last 30 years (regression quantiles greater than zero). This result is consistent with the idea that conversion of relatively homogeneous habitats (e.g., forests, agriculture) into more heterogeneous landscapes favor different species, which combined with introductions of exotic taxa raise larger-scale species richness (e.g., Schipper et al. 2016, Jarzyna and Jetz 2018). Note, although our approach examining scale-dependent diversity responses was similar to that reported by Jarzyna and Jetz (2018) also using the BBS dataset, our results differed slightly from theirs. Specifically, Jarzyna and Jetz (2018) found increases in species richness from their smallest scales (50 km^2) which increased at the scale of the entire continent, consistent with the pattern of differentiation we found at this scale. However, when Jarzyna and Jetz (2018) extended their analysis to include global extinctions, this necessarily lead to a subsequent decline in richness from the continental to global scale, more in line with the hump-shaped predictions in Box 1.

Hawaiian Passerine Birds— The bird fauna of the Hawaiian archipelago is a classic example of unique adaptive radiations as a result of their remoteness, as well as devastating extinctions at the hands of humans, both directly via hunting, and indirectly via the introductions of many exotic species. We compiled data from Pyle and Pyle (2017), comparing species that invaded and went extinct since colonization of Europeans (~200 years; we do not consider extinction that occurred due to humans prior to European contact) and included only data from passerines from the 6 largest islands (Kauai, Oahu, Lanai, Molokai, Maui, Hawaii) to avoid undue influence from marine species (see also Sax et al. 2002). This case study is based on checklist data rather than survey data, but islands can be nested within the archipelago for a scale-explicit analysis, as presented in Figure 2C. Here, we analyzed data for three nested scales: (1) the scale of a single island (islands differ considerably in area and so vary along the x-axis); (2) by

combining the two most northerly islands (Oahu and Kauai), the three central islands which make up the Maui Nui complex that was connected ~200,000 years ago (Maui, Lanai, and Molokai) (we did not nest the largest island, Hawaii, at this scale because it is so large); (3) by combining all six islands into a single archipelago-wide estimate. For each scale, we calculated the log-ratio of species richness change (hereafter LRS).

At the scale of each island, we find large increases in species richness over the considered time period (i.e., lower confidence interval is well above zero). Indeed, it is well known that introductions of bird species far exceed extinctions on these islands, leading to a net increase in species richness at the hands of humans (e.g., Sax et al. 2002, Lockwood 2006). However, when we nested islands into groups, this pattern became less dramatic. Even though individual islands gained many more species (average of 19 species) than they lost (average of 6.5 species), this pattern was reversed at the scale of the entire archipelago with a slight reduction in species richness over time (29 species went extinct archipelago-wide, while 27 species invaded). This pattern was consistent with the 'flip-flop' scenario in Box 1, whereby gains of invaders were widespread (average range of invading species was 4.07 islands), but these gains were tempered at larger scales because of homogenization, due to the extinctions of small-ranged (island endemic) species (average range of extinct species was 1.2 islands).

European plants— We used species lists of plant extirpations (based on national Red Lists) and invasions (from the DAISIE database) from Europe, compiled at the country level (see Winter et al. 2009 and Ellis et al. 2013 for details). We analyzed data at three nested scales based on proximity and natural geographic boundaries (Table S1): (1) country; (2) subregions consisting of geographically proximate countries; (3) regions consisting of proximate subregions; and (4) the entire continent. For each scale, we calculated the LRS based on the country level species lists.

In this case, we found that species richness increased through time, but that the overall pattern of species richness change across nested scales did not show a clear signal (Figure 2D). If this pattern is likely, it would be consistent with the scenario discussed in Box 1, where there is no homogenization or differentiation, and thus no scale-dependence in species richness change. However, there is considerably more variance and higher increases in species richness at intermediate scales (relative to lower or higher scales), suggesting a possible hump-shaped relationship more consistent with the scenario in Box 1 (with so few groupings at larger scales, there is not enough power for such an analysis).

Towards a synthesis of temporal change in species richness across scales

We hope that we have made it evident that spatial (and temporal) scale is a critical feature that influences the magnitude and direction of species richness change. Any syntheses of species richness change, thus, will be greatly enhanced by an explicit consideration of scale. However, it remains unclear how straightforward it will be to incorporate scale into future analyses and meta-analyses.

One hypothesis is that we would be unlikely to observe any signature of scale in a compilation of heterogeneous data collected on disparate taxa and systems. This is because, as we illustrated above, there are a range of possibilities for how scale-dependence can emerge depending on features that are likely to vary among studies, taxa and systems. For example, dispersal or introduction rates, which vary greatly among taxa (e.g., birds versus mollusks) and systems (e.g., islands versus mainlands), influence the magnitude of species richness change through time, as well as the scale-dependence of this change. Likewise, the magnitude and direction of species richness change and its scale-dependence will depend on whether a system returns to a quasi-equilibrium following disturbance or human impact (Figure 1). If all, or even some, of these possibilities were equally likely, they would obscure any clear pattern from

observations across taxa, systems and scales since the contrasting results would cancel each other out.

Alternatively, it could be that across studies and scales, there is a predominant signature of scale-dependence that emerges. For example, many authors have suggested that small (or negligible) changes in species richness at small scales are exacerbated at larger scales via biotic homogenization due to regional and global extinctions (e.g., McKinney and Lockwood 1999, Sax and Gaines 2003, Cardinale et al. 2018). However, other authors have suggested that the overarching pattern of species richness change should be hump-shaped with scale first increasing from to intermediate scales due to the spread of non-native species, and then decreasing from intermediate to large scales due to extinctions(e.g., Cassey et al. 2006, Thomas 2013, Vellend et al. 2017a, Primack et al. 2018).

In what follows, we present the outline of an approach that may help address whether there is general consistency in the scaling relationships of species richness change through time. Importantly, however, our compilation and analysis are by no means complete, but rather just the beginning of a much more intensive investigation which we hope may be inspired by this Forum piece. Our exploration began with the collation of a large dataset of species richness change through time from local to global scales and across several taxa (for details, see Appendix 3). Specifically, we combined two types of data. (1) At typically small spatial scales, we pooled three databases (Vellend et al. 2017b, Dornelas et al. 2018, Elahi et al. 2015) that consisted of local measurements of species richness from a variety of ecosystems through time. These data all involved some form of repeated surveys of individuals over time. (2) At regional scales, we compiled a database consisting of studies where species richness could be discerned from two points in time —typically a long time period spanning the range of smaller versus higher levels of human impact. These were typically species checklists from nature parks and natural areas, geopolitical regions (e.g., states, countries), or other biogeographic

boundaries (e.g., continents, islands). Such checklist compilations have often been used to determine long-term trends of introductions/extinctions (e.g., Sax et al. 2002, Winter et al. 2009, Essl et al. 2013). These two distinct sources of data raise clear issues discussed below.

For each time-series from this combined dataset, we calculated the log ratio of species richness (LRS) between the first and last observation of species richness ($\log(S_T/S_1)$; intermediate time points were ignored) and estimated the spatial extent of the study. We coarsely separated data into taxonomic and habitat groupings (e.g., terrestrial plants, marine fish) which were analyzed separately. This is because we felt that combining taxa and ecosystem types into an overall analysis was not sensible because these groups are not expected to respond to spatial scale in the same way. For example, owing to differences in body size, dispersal capacity, and other features, we would expect colonization rates, extinction rates and other features of the taxa to dramatically influence whether, and how, scale-dependence emerges (see Appendix 1). However, even within taxa, we expect a great deal of heterogeneity depending on the landscape in which observations are made (e.g., the diverging patterns observed among birds in North America [Figure 2B] and Hawaii [Figure 2C]). Since our intention is simply to expose the nature of the scale-dependence problem, we performed only exploratory analysis of these data, which we discuss in more detail in Appendix 3.

In Figure 3, we illustrate how the LRS varied as a function of the spatial scale on which the study took place for four taxa for which we had enough data to provide meaningful illustration—terrestrial plants, terrestrial birds, terrestrial mammals, and marine fish (other taxa for which we had data are also presented in Appendix 3). A few interesting patterns emerge. First, the variation in LRS was quite high at smaller scales, but with an average change centered on zero, in line with previous meta-analysis (e.g., Vellend et al. 2013, Dornelas et al. 2014, Elahi et al. 2015, Blowes et al. 2018). Second, for most taxa, increases were more prevalent than decreases at intermediate to large scales. This is consistent with the notion that increases in

habitat heterogeneity and/or species invasions lead to increases in species richness at these intermediate to large (roughly regional) scales (e.g., Sax et al. 2002, Winter et al. 2009, Jarzyna and Jetz 2018). Indeed, when we combined data from all studies and made scale binary, where studies on local scales are defined as those $\leq$10 km^2 and those on regional scales are defined as those >10 km^2, a Wilcox non-parametric test shows that the LRS is significantly higher at the regional scale (i.e., an average gain of species) than for studies at the local scale (i.e., no net change) ($p<0.001$). While the choice of 10 km^2 as a cutoff is arbitrary and may vary depending on the body size and dispersal ability of different taxa, the same results emerge if this cutoff is varied by several orders of magnitude. This is consistent with the idea that even if small-scale species richness change is zero or negative, biotic differentiation due to habitat heterogeneity and/or alien species can lead to smaller negative effects and/or positive effects at larger spatial scales. In addition, for both terrestrial birds (Figure 3A) and terrestrial plants (Figure 3B), we see patterns consistent with the notion of a hump-shaped scale-dependent relationship with significantly negative quadratic terms with LRS first increasing, and then declining again at the largest spatial scales where regional and global extinctions play a stronger role (see also Jarzyna and Jetz 2018; Appendix 3). We did not observe any clear signals for the other taxa, though acknowledge that data limitations are likely a reason.

We emphasize that these data and analyses are meant to be illustrative of the problem of incorporating scale into synthetic analyses of species richness change, and how one might approach it, rather than to provide any definitive conclusions. Even if a signal of the influence of scale can be discerned from Figure 3, there is a great deal of variation that is not captured by simple patterns. Furthermore, at present we do not attempt to disentangle differences in methodology and/or time scale for each study. For example, larger scale studies are typically based on checklist data and occur over longer time periods, and thus confound spatial and temporal scales (Figure S1). Despite these complexities, we hope this analysis accomplishes

two goals: (1) illustrate why different studies performed with different methods and at different scales can give very different answers to a seemingly simple question of whether (and how) species richness changes through time; (2) emphasize that scale-dependent species richness change will require a more sophisticated approach to studying species richness change in order to understand past species richness change, and potentially predict future changes.

Conclusions

There is no *a priori* reason to expect that losses of species richness at the global scale trickles down to losses of species richness at regional and local scales, nor is there an *a priori* reason to expect that any changes (or lack thereof) in richness at local scales should be reflected in regional and global trends. Here, we have presented a three-pronged narrative regarding the issue of scale-dependent richness changes using simulation models, case studies, and a collation of heterogeneous data. We show that the nature of scale-dependence need not be as simple as usually depicted, and that instead, any change in species richness can remain the same across scales, can increase with scale, can decrease with scale, or can be unimodal with scale. A deeper understanding of the features of how and which species respond to changing conditions is necessary in order to more fully understand and predict this scale-dependence.

From our analyses above, it seems clear that incorporating scale into analyses of species richness and its change will be much more complex than simply incorporating the scale of the study as a covariable into synthetic analyses. Instead, we advocate that it will be necessary to establish new analytic tools that can explicitly measure the scaling of diversity, and how that scaling changes through time, along the lines of the species-area relationships (SARs) discussed in Box 1. This will likely require the gathering and analysis of nested scale-explicit data, such as from the case studies above, or the development of novel analytical tools that can capture changes in species richness in a scale-explicit way. For example, Keil and Chase (2019) have recently shown how scale-heterogeneous data can be combined into a single

predictive framework on how species richness changes due to environmental and biogeographic factors using the concept of SARs. While their approach focused on patterns at a single point in time, it could be extended to include comparisons of SARs between time periods to evaluate the nature of scale-dependent species richness change. There is no doubt that this is a much more difficult endeavor than what has been accomplished to date, but one which we argue is essential if we hope to understand and predict how species richness is changing, and will continue to change, at the hands of human activity.

In our discussion, we have almost exclusively focused on changes in species richness through time. This is because species richness is the most frequently used metric to evaluate patterns of biodiversity and its change, especially in response to anthropogenic impacts. This makes some sense, as species richness is the ultimate currency in which many scientists and conservation managers are most interested. However, species richness is a notoriously unreliable metric of change, often being quite insensitive to dramatic changes in the abundance and composition of species in a community (Dornelas et al. 2014, Supp and Ernest 2014, Hill et al. 2016, Santini et al. 2017, Hillebrand et al. 2018). Therefore, it is important to keep in mind that quantifying species richness change (or lack thereof) is only one measure of a much more complex phenomenon of biodiversity change through time and space. Additionally, we have only focused on change in taxonomic patterns of richness, and it is possible that other facets of diversity, such as functional and phylogenetic diversity, can differ in how they change across scales in response to environmental change (e.g., Knapp et al. 2017). Nevertheless, it is also clear that scale can strongly influence measures of taxonomic diversity other than species richness (e.g.; Lande 1996, Dauby and Hardy 2012), as well as functional and phylogenetic metrics (e.g., Morlon et al. 2011, Smith et al. 2013, Jarzyna and Jetz 2018). Thus, adapting this scale-explicit perspective would be highly relevant for other measures of biodiversity and its change, as well as the ecosystem-level services associated with this biodiversity.

Because species richness scales non-linearly with increasing area, and because environmental changes such as those caused by human activities can influence species colonizations and extinctions differentially, we should often expect a complex response of species richness change to human activities across scales. As a result, we argue that scientists interested in biodiversity change and its potential consequences should change their perspectives from one focused primarily on measures of species richness and a largely agnostic perspective on scale, to one focused more explicitly on understanding how and why species richness changes across spatial and temporal scales. To do so will require a more concerted effort to monitor and analyze biodiversity and its change in a more scale-explicit way.

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Data Availability: All the data and code for this manuscript will be made available on FigShare.

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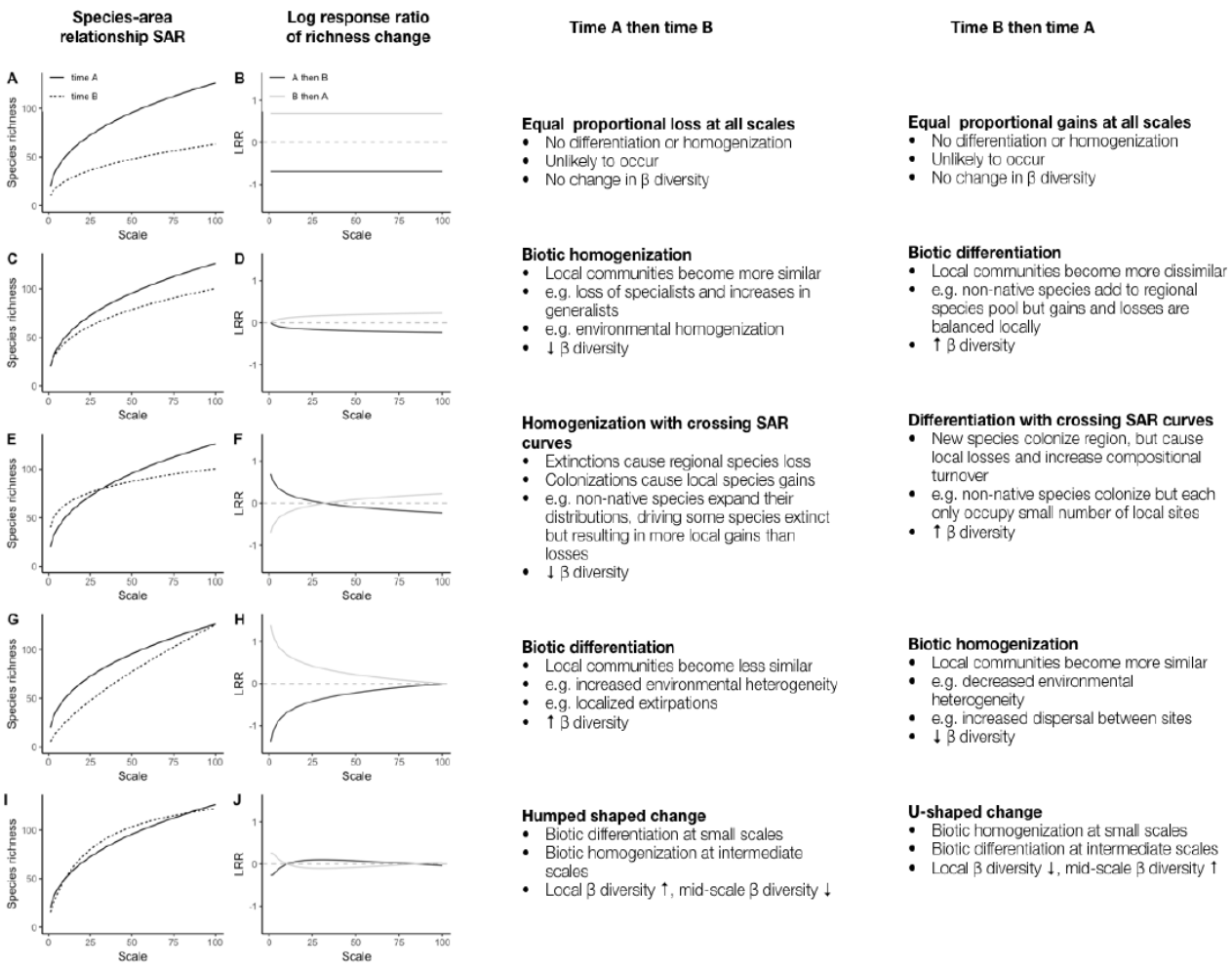
Box 1. **Conceptual overview of scale-dependent species richness change through time**

We illustrate how species richness can change through time by varying parameters of the power-law species-area relationship (SAR), $S=cA^z$ (where S is species richness, A is area, and c and z are constants) and simple derivatives of it, shapes of the SAR between two time periods. This can also be directly linked to the concept of diversity partitioning (γ-diversity=α-diversity∗β-diversity) and the influence of biotic homogenization and differentiation through time (e.g., Crist and Veech 2006, Scheiner et al. 2011, Socolar et al. 2016).

The figure below illustrates several qualitatively distinct ways in which the balance of species gains and losses (=net change in richness) through time can change from local to global scales. In each case in the figure below, the solid line represents the SAR from one point in time, and the dashed line represents the SAR from a different point in time. The largest scales in these comparisons need not be global, and instead can represent differences in regional species richness, which can decrease via range contractions or local extirpations, or increase via introductions or range expansions. For completeness, the two time periods (A and B) can be reversible; Time A can be 'pre-impact' and Time B can be 'post-impact', or vice versa.

In each of the first four cases of the figure, we vary the two parameters (c and z) in the SAR between the two time periods, and compare the log response ratio difference in species richness between the two time periods. In the final case, we changed the power law form of the SAR to have a saturating shape (i.e. $S = c + AS_{max}/(k+A)$, where S_{max} is the saturation value for species richness, and k is the area at $S = 0.5S_{max}$). (Note, we are not arguing that SAR curves should be saturating, but rather use this shape simply to illustrate how homogenization and differentiation can simultaneously operate at different scales). By simply changing the parameters of these models, we show how species richness change can increase, decrease or

remain the same through time, and how the magnitude of this change can increase, decrease or be unimodal across spatial scales.



Conceptual figure illustrating different hypothetical scenarios of biodiversity change and their relationship with spatial scale: equal proportional change (A, B), greater regional than local change (C, D), crossing SARs (E, F), greater local than regional change (G, H), and double crossing SARs (I, J). The left column (A, C, E, F, I) shows species-area relationships (SARs) at time A (solid line) and time B (dashed line) a hypothetical change. The right column (B, D, F, H, J) shows the log response ratio (LRR) of this change (i.e. $\log(S_{after}/S_{before})$), where the black line corresponds to the scenario of time A then B and the grey line is time B then A.

Table 1. Brief summary of case studies.

Geographic Region and Taxa	Range of Scales	Data type	Temporal Range	Reference
Central American corals	$1m^2$ plots nested within transects across sites and regions	Surveys	5 years	Gomez et al. (2017)
North American Breeding Bird Survey (BBS)	~40km routes nested within 20^o x 25^o grid	Surveys	30 years	Sauer et al. (2017)
Hawaiian Passerine birds	Single island to entire archipelago	Checklists	~200 years	Pyle and Pyle (2017)
Plants in Europe	Single country to whole continent	Checklists	~500 years	Essl et al. (2013)

Figure 2.

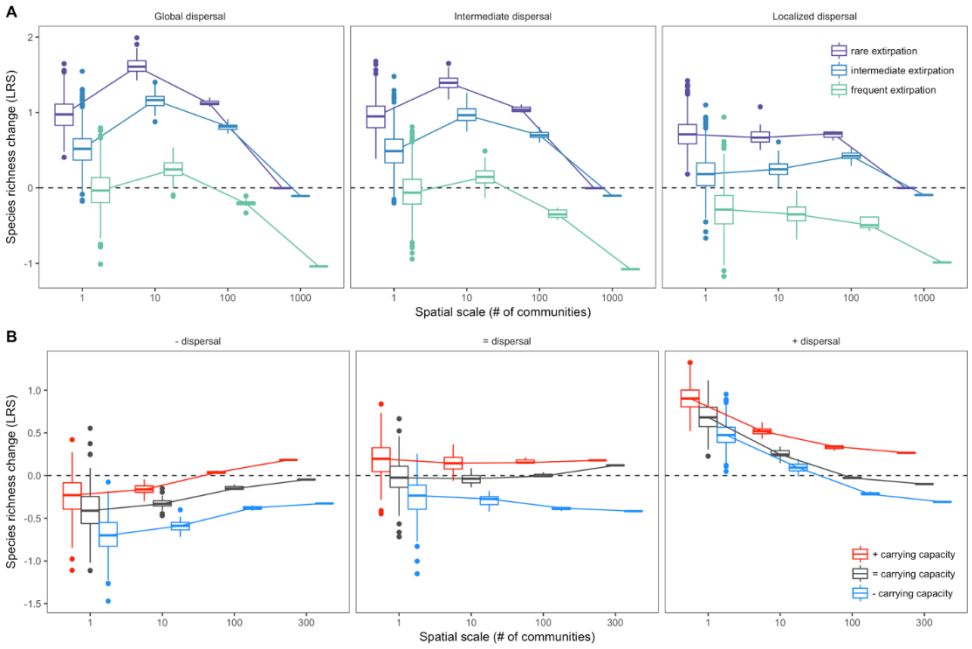


Figure 1. Species richness change at 4 spatial scales in the two simulation models. Panel A shows the non-equilibrium model and panel B shows the equilibrium model. In panel A, scenarios of dispersal scale are arranged by column (global – dispersal is equally likely between all local communities; intermediate – dispersal is somewhat constrained within nested spatial scales; localized – dispersal is highly constrained within nested spatial scales). The colors contrast three different scenarios of local extirpation frequency (rare, intermediate, and frequent). In panel B, scenarios of dispersal change are arranged by column (decreased, no change, and reduced dispersal compared to the pre-equilibrium conditions). The colors contrast different scenarios of carrying capacity change. In both panels, box plots show the range of variation at a given spatial scale in the simulation. Boxplots are offset to avoid overlap, but all scenarios were conducted at the same spatial scales in each model. The solid lines connect the median values for each spatial scale. Both panels show results from a single representative run of the simulation.

Figure 2.

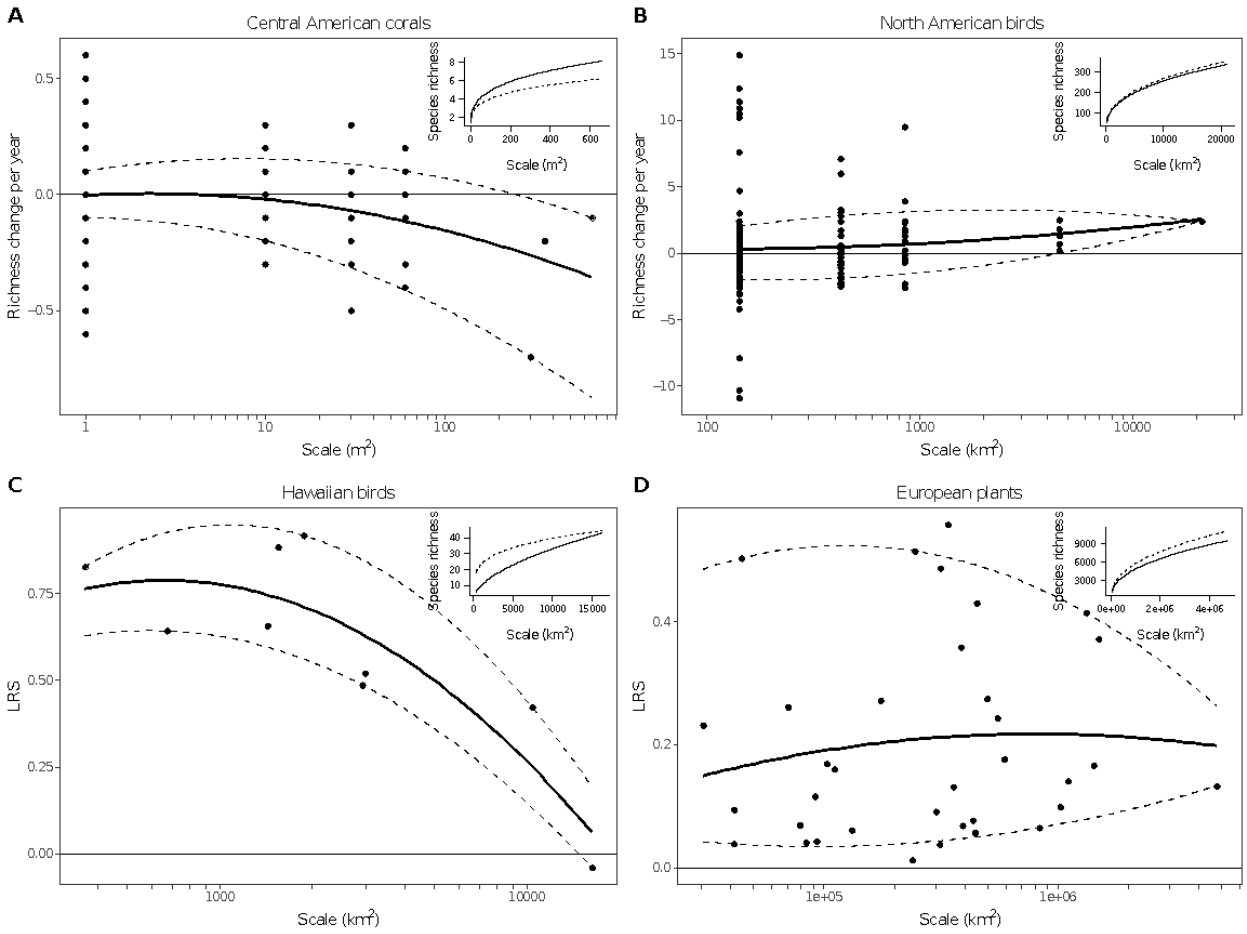


Fig. 2. Results from case studies where species richness change was measured on a yearly basis from surveys (A and B), or as the log ratio of species richness change (LRS) from checklists before/after intense human activities (C and D). A brief description of each case study is in Table 1, and more detail methods are given in Appendix 2. Points are nested so that the smallest scale is nested within the next largest scale. For surveys (A and B), scales are discrete, while for the check-lists (C and D), scales are more continuous because countries and islands differ in size. In each case, the solid line is the fit from a quadratic ordinary least squares regression and the dashed lines are the 10 and 90% quantiles from this model. Richness

change patterns for: A) Central American corals over 5 years, where $1m^2$ quadrats are nested within transects, sites, and entire regions; B) North American Breeding Bird Survey (BBS) over 30 years where routes were aggregated into increasing degree grid sizes (the scale on the x-axis is the sum of the areas on each route); C) Hawaiian bird species since European colonization (~200 years) of the archipelago taken from checklists of native, extinct and exotic species. Rightmost circle represents the combined trend in richness of the 6 largest islands, while the circles to the left represents the trends on each island; and D) European plant species richness over several centuries of increasing human impact (~500 years) by including native, extinct, and alien species lists from countries and nesting those within sub-regions, regions, and the European continent. Slopes for each relationship are given in the panels; significance tests for the slopes are discussed in Appendix 3. Insets show the corresponding SAR curves from the start (solid line) and end (dashed line) of the time-series comparisons estimated using non linear regression with the form y= a+x^z.

Figure 3.

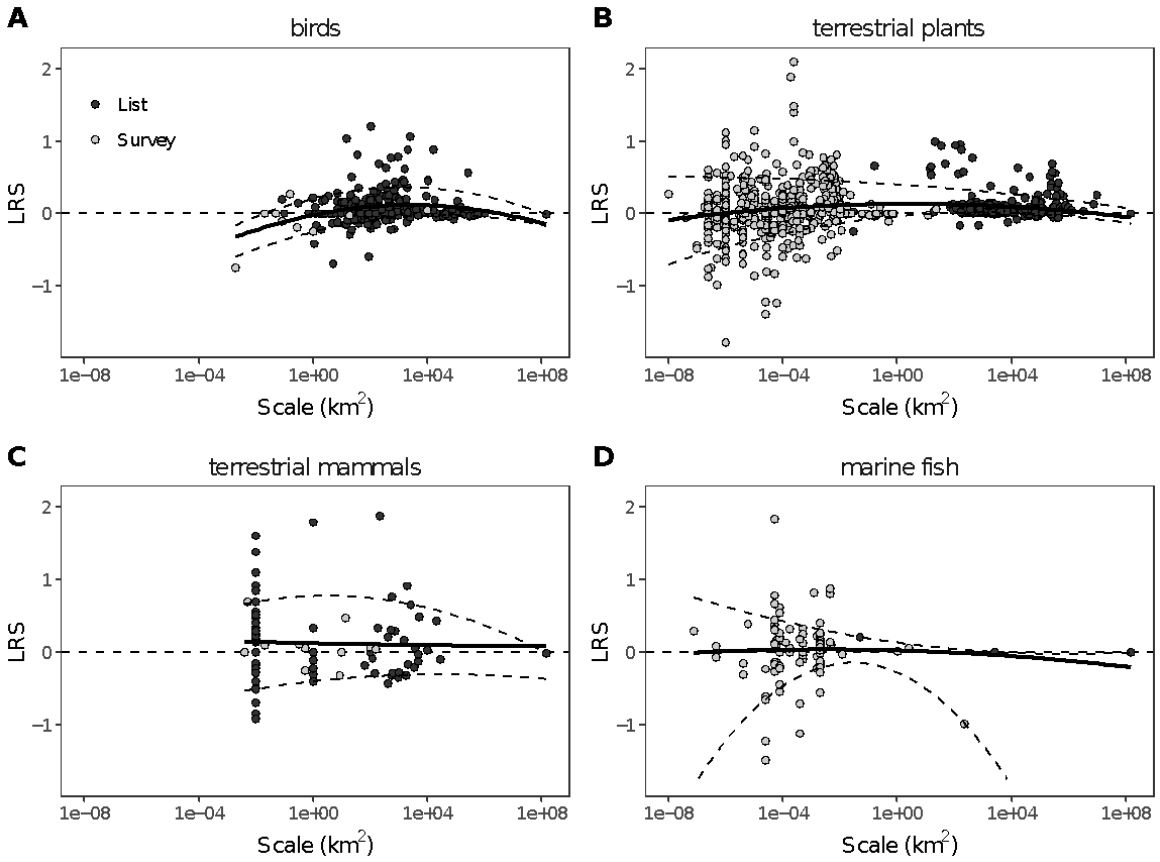


Figure 3. These figures show a plot of LRS (log ratio of species richness) vs log spatial scale, indicating trends (positive is an increase, negative a decrease in richness). Light circles are survey-based data. Dark circles are checklist-based data. Data are presented for A) terrestrial birds , B) terrestrial plants , C) terrestrial mammals , and D) marine fishes . In each case, the solid line is the fit from a quadratic ordinary least squares regression and the dashed lines are the 10 and 90% quantiles.

APPENDICES:

Appendix 1: Methods and results for representative simulation models

Methods for Non-equilibrium model. First, we used a non-equilibrium model similar to that used by Cassey et al. (2006) to address similar questions. Such a non-equilibrium scenario may be a reasonable assumption for many systems over the past several hundred years as anthropogenic pressures continue to increase through time. Specifically, we modelled the effects of immigration and population losses in a simulated, spatially structured metacommunity to explore the scale-dependence of species richness change through time. In our simulation, we assumed that changes in species richness are only due to probabilistic local population loss and immigration events from the regional species pool. Therefore, the simulation serves as a null expectation for how biodiversity change should depend on spatial scale in the absence of speciation, trait differences and/or habitat heterogeneity.

We simulated a global metacommunity consisting of 1000 local communities, nested equally within three larger scales of communities at four spatial scales. Therefore, we have 1 global metacommunity consisting of 10 regions, each consisting of 10 sub regions, that each consist of 10 local communities. We initially seeded this global metacommunity from a pool of 1000 species (Figure S1) such that:

1. The species pools for each of the 10 regions were drawn at random from the global pool with a 0.3 probability of selecting each species.
2. The species pools for each of the 100 sub regions were drawn from drawn at random from the species pools in region in which they were nested, with a 0.3 probability of selecting each species.

3. The species pools for each of the 1000 local communities were drawn from drawn at random from the species pools in sub region in which they were nested, with a 0.3 probability of selecting each species.

After seeding the metacommunity, we removed all species from each nested community that were not present in at least one of the component local communities. This resulted in only a subset of the 1000 species being present in the metacommunity. This initial seeding of the metacommunity served as our pre-change condition, to which changes in biodiversity that resulted from colonization and extirpation events are compared.

Following the initialization of the metacommunity we simulated biodiversity change over 100 time steps. During each time step, in each local community:

1. Species *i* colonizes the focal community with a probability: $p_{ic} = 0.01\left(\frac{A_{is}+A_{ir}k+A_{ig}m}{\sum_{j=1}^{S} A_{js}+A_{jr}k+A_{jg}m}\right)$, where A_{is} is the number of communities in the same sub region occupied by species *i*, A_{ir} is the number of communities in other subregions within the same region occupied by species *i*, and A_{ig} is is the number of communities in other regions occupied by species *i*. A_{js}, A_{jr}, *and* A_{jg} are represent these same values but for each other species *j*. *k* and *m* are scaling parameters that determine the degree to which dispersal is constrained within nested subsets of the metacommunity.
2. Species *i* is lost from the focal community with a probability $p_{il} = p_l * ext_i$, where p_l is the local extirpation frequency, and ext_i is the extirpation probability for species *i*. Values of *p* were drawn at random from a beta distribution ($\alpha = 2$, $\beta = 5$), such that some species were more prone to extirpation than others. This parameter ext_i was the only non-neutral component of the model.

Species were only lost from large spatial scales when they were lost from all nested communities comprising that region. We considered three patterns of dispersal (global: k = 1, m = 1; intermediate: k = 0.1, m = 0.01; localized: k = 0.01, m = 0.001) crossed with three scenarios of local extirpation frequency (rare - p_l = 0.01; intermediate - p_l = 0.03; frequent - p_l = 0.1). In all scenarios, the colonization probability p_c was set to 0.001. In each simulation, we calculated species richness change from the initial conditions for all communities at all four spatial scales using the log response ratio.

Methods for Equilibrium Model. To contrast with the non-equilibrium scenario above, we used an individual-based neutral model, following Hubbell (2001), to simulate a metacommunity in quasi-equilibrium. This quasi-equilibrium is achieved because probabilistic extinctions are slow and are balanced out by rare speciation events.

We simulated a global metacommunity consisting of three regions, each containing 10 subregions, each comprised of 10 local communities. The local communities each contain *J* individuals. In each time step, *D* individuals die in each local community, chosen at random. Then:

1. With a probability (*1-m-v*) replace the individual with a copy of another drawn from the remaining local community
2. With a probability (1-*v*) replace the individual with an immigrant drawn from the metacommunity, weighted by nested structure of the metacommunity such that:
    a. *1-m* is the probability that the parent of the immigrant is from another community in the same subregion.
    b. m-m^2 is the probability that the parent of the immigrant is from the same region, but not the same subregion.

c. m^2 is the probability that the parent of the immigrant is a different region of the metacommunity.

3. With a probability (*v*) a new species is born

We started the simulation by assuming that all individuals in a local community are the same species and the identity of these species differs for each local community. We started the simulations with the following parameters: $J = 50$, $D = 5$, $m = 0.1$, and $v = 0.005$. We then ran the model for 1000 time steps, which is sufficient to allow biodiversity at all scales in the metacommunity to reach equilibrium (no long term directional changes in biodiversity). We then simulated some change to influence biodiversity change by changing *J*, *m,* or both and then ran the model for an additional 1000 time steps to allow biodiversity to reach a new equilibrium.

We explored the following scenarios in a factorial contrast:

1. a reduction or increase in carrying capacity – reduced or increased *J* by 10
2. an increase or decrease in long distance dispersal – increased *m* by 0.2, or decreased *m* by 0.05

Again, one could exhaustively explore other parameter values, but we felt that this was sufficient to produce a range of biodiversity change patterns that differ in how they depend on scale. We then estimated biodiversity change for each local community, subregion, region, and the entire global metacommunity as the mean richness of the final 100 time steps before and after the parameters were changed using the log response ratio of pre-change and post-change equilibrium species richness as above.

Appendix 2.

Analyses for case studies—For each of the case studies presented above, we nested smaller scale surveys (in the case of corals and breeding birds) or regional checklists (in the case of Hawaiian birds and European plants) into larger aggregate surveys or checklists. This allowed us to compare species richness change at multiple nested spatial scales; change was measured yearly for the surveys, and as a log-ratio comparing species richness at time 1 and time 2 for the checklists. Because there are more observations at smaller scales than at larger scales (which have several smaller-scale estimates nested within), simple OLS regression of species richness change regressed against scale may be considered an overly liberal test of the significance of the slope, and thus we chose not to present p-values in the text, as the quantile regression fits illustrate the patterns in the data we wish to highlight.

Nevertheless, analyses in the macroecological literature often use regression-based approaches on data with similar nested structures (e.g., hundreds to thousands of studies on nested species-area relationships), and thus we used simple regressions simply to illustrate the scale-dependence of the relationships. Corals showed a significant slope negative slope and quadratic term ($P<0.01$). The quadratic model was not significant for the North American birds ($P=0.25$) but a linear model showed a significant positive slope with scale ($P<0.01$). The Hawaiian birds showed a significant negative slope ($P=0.02$) and a marginally significant quadratic term ($P=0.09$). The European plants did not show a significant relationship with scale. When we used a more conservative approach, taking only the means at each scale (and circumventing the nesetedness problem) and fitting a linear model, the relationship was still significant for the North American birds ($P<0.01$); however, because there were only 5 scales analyzed in the coral case study, we had less confidence that the slope was negative ($P=0.18$). We did not fit this conservative approach to the Hawaiian Birds because this would leave us with two few scales for appropriate analysis. When we averaged the LRS and area at the

country, region, and subregion scales, the European plants showed a marginally significant negative slope (-0.03) with scale ($P<0.08$).

Table S1. Regional classification of European countries used in the European plant case study.

Country	Subregion	Region
Austria	Central	Western
Baltic States	Baltic	Northern
Belgium	Central	Western
Bulgaria	East South	Eastern
Czech Republic	East North	Eastern
Denmark	Scandinavia	Northern
Finland	Scandinavia	Northern
France	Central	Western
Germany	Central	Western
Greece	Mediterranean	Southern
Hungary	East South	Eastern
Iceland	Scandinavia	Northern
Ireland	British Isles	Western

Italy	Mediterranean	Southern
Netherlands	Central	Western
Norway	Scandinavia	Northern
Poland	East North	Eastern
Portugal	Iberia	Southern
Romania	East South	Eastern
Spain	Iberia	Southern
Sweden	Scandinavia	Northern
Switzerland	Central	Western
United Kingdom	British Isles	Western

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Appendix 3: Methods for building cross-scale dataset

In all, we present the log ratio richness change from 1429 data sources collated from a number of different sources (see below). All data and sources are available at https Figshare link..

Local scale richness change estimates— We developed a synthetic dataset to examine species richness change through time across taxa and spatial scales from local to the nearly global scales. The dataset consisted of two qualitatively distinct types of data. First, we used data from relatively local-scale ecological surveys that were taken over 2 or more time periods, typically on the order of decades. This includes data included in Vellend et al. (2017b) on plants, Dornelas et al. (2014) and the expanded BioTIME database (Dornelas et al. 2018) on a number of different taxa, and Elahi et al. (2015) on marine organisms. Although these datasets were heterogeneous in their focus, habitat, taxa, temporal scale, and measurements (i.e., species richness versus composition), they all share in common quantification of species richness for at least two time periods with consistent methodology.

From these datasets, we extracted time-series that met the following criteria: 1) sampling methods were consistent over time, and this was assessed based on information available in the original studies, 2) the sampling area (grain size of sampled units, m^2) was clearly reported as well as number of samples, and 3) the sampling location had to be consistent over the duration of the time-series. For the purposes of this study, we only used the first and last estimates of species change to calculate the log ratio difference in species richness (LRS). Thus, for each study, we had a single estimate of species richness change.

We considered the total sampled area reported across all replicates within that time-series to assign a spatial scale (area) to each diversity estimate. When multiple estimates were reported within a single time and region, we aggregated the sampled areas by adding the area and the species lists to estimate a (pooled) species richness per (aggregated) sampled area. When

estimates were based on reported sample based rarefaction estimates, the total sampled area was calculated as the size of each sampled area multiplied by number of samples used for the rarefaction. In no case did we estimate species richness for unsampled areas. Combining sampled area and diversity data from different sampling locations that were not adjacent to each other in this way introduced uncertainty associated with how species are aggregated in the landscape (e.g., Azaele et al. 2016). This method of pooling areas might overestimate diversity by ignoring spatial beta diversity for cases where species are distributed non-randomly across a site. However, this uncertainty was preferable to uncertainty associated with the alternative approach of extrapolating observed species diversity to unobserved areas.

Larger-scale checklist data— We augmented the above data with additional estimates of change from a qualitatively distinct kind of data to expand the range of taxa and spatial scales in our analyses. This came from a literature review of species richness estimates (or lists of species presences/absences) and its change over (typically) long time periods (decades to centuries). We identified studies by searching the literature (Google scholar, ISI) using search terms including, but not limited to, “resurvey”, “historic”, “extinction”, “alien”, “invasion”, “richness”, “change”, and “turnover”. In addition, we located data from existing species inventory databases (e.g., state, province or national check- and red lists, protected area checklists, IUCN redlists, NatureServe, USDA plants) where information on historical and current richness is available, as well as extinctions and colonizations. Finally, to fill biogeographic, taxonomic, and spatiotemporal gaps, we added datasets opportunistically and conducted more targeted searches (i.e., located via personal networks, gray literature, or using more specific search terms to target specific groups).

For each dataset, we recorded the taxon, location, total spatial grain and extent sampled based on what was reported in the original study (km^2) (or taken from other sources, such as for the size of geopolitical units (e.g., area of country) or biogeographic units (e.g., area of islands or

continents), and the years in which each sample was taken. For many datasets, year was estimated between long time periods (e.g., before human colonization or expansion). We recorded species richness at each point in time (or in several cases, estimated this from numbers of extant, extinct and nonnative species), and calculated LRS as above.

Appendix 4: Analyses of cross-scale data

As noted in the main text, this analysis was done in the spirit of an exploratory analysis because we *a priori* would not expect any single model structure to fit all of the data, and instead, we expected that different systems would exhibit different kinds of scale-dependence. We report p-values and AIC values only as a courtesy. Several irreconcilable statistical issues as well as a lack of clear *a priori* hypotheses prevented a full hypothesis testing analysis. For each taxon group analyzed such as terrestrial birds or marine fish, we analyzed LRS ($\ln(S_{last}/S_{first})$) vs scale (area in m^2). This gives a common measure of change across datasets with a roughly normal distribution. Within each taxonomic group (where more than 40 data points were available), we ran several regression models:

A. Intercept Only – calculated the mean and standard deviation and a test to see if the mean LRS was significantly different from zero using a t-test;

B. Linear OLS – a simple linear regression of the form LRS~$\log_{10}$(scale). We report only the coefficient for scale (determine if LRS changed with scale) and the p-value from the t-test for this coefficient;

C. Quadratic OLS – of the form LRS~$\log_{10}$(scale)+($\log_{10}$(scale)-mean($\log_{10}$scale))^2;

D. Quadratic OLS with Study type - of the form LRS~$\log_{10}$(scale)+($\log_{10}$(scale)-mean($\log_{10}$scale))^2+StudyType (where study type was a binary dummy variable coded as 0 for lists and 1 for surveys);

E. Quadratic GLS – because variance was non-constant, a weighted GLS model (with MLE) was used. The variances appeared to vary in a non-monotonic fashion across scale (Figure 2) so there was no obvious appropriate error model, but we used var~exp(k*$\log_{10}$(scale)) with the fixed terms as in model (C).

We report both the estimated coefficients and the p-values of individual coefficients based on their t-tests (Table S2). We compared the AIC of model (C) with (E) to see which variance model was best. We have not done a full model selection, nor a full p-value analysis (e.g. comparing quadratic to linear or adjusting for multiple tests) because they would be misleading and overreach the nature of these highly heterogeneous data. Additionally p-values are of limited meaning when there are large numbers of data points, but low explanation of the variance by models as in our data. We therefore report p-values (and some AIC values) but we limit the strengths of our interpretations accordingly.

Table S2 presents the results from our analyses of all of the data collected. However, we caution that analyses of some of the taxonomic groups are not likely very meaningful. For example, several taxa had few observations (e.g., marine plants, terrestrial invertebrates, freshwater fish), were difficult to compare/calculate area (e.g., freshwater fish from a single lake versus entire regions with only a small percentage of land area covered by freshwater), or had few observations at large scales that typically involved checklists (e.g., marine invertebrates). Thus, even though we present all of our analyses in Table S2, Figure 2 only illustrates the results for the four taxonomic groupings that we were most confident in the data being representative to allow a reasonably comparative approach (note, marine fishes also had few observations from checklists at larger scales, but we included them as a marine example).

Note the following three points argue against overly strong interpretations of these data: 1) There are large numbers of data points; even relationships with low explanatory power (R^2

values often around 0.01) were still statistically significant. 2) The variance is clearly not homoscedastic with spatial scale, but has a complex structure. In Figure 2, the variation often appears hourglass shaped (two bulges), probably driven by the data sampling intensities at different scales. This makes choice of a model for the variance structure difficult and does not conform to any of the standard models (e.g. power law or exponential function of x-variable). 3) The factors of potential interest are highly confounded (e.g., spatial and temporal scales) (Figure S1): a) the Pearson correlation between log-transformed spatial scale and temporal duration of the time-series ($r=0.756$; $p<2e\text{-}16$); b) Welch's two-sample t-tests for log-transformed scale separated into data collection methods (surveys versus checklists) was also highly significant (means of $10^{-4.36}$ vs $10^{2.37}$ respectively); and c) a similar t-test for log-transformation of duration of the time-series versus study type was also significant ($10^{1.44}$ vs $10^{2.37}$ years). Models (C) and (D) were qualitatively identical (quadratic terms were significant or not significant the same in both models) so only model (D) is reported in Table S2. Similarly model (A) is a better estimate of the mean height of the data so intercepts are not reported in the other models.

Recognizing these qualifications, our analyses summarized in Table S2 indicate several scale-dependent responses, often at least roughly consistent with the non-linear expectations presented in the main text. However, there is also a great amount of variation in LRS within and among taxonomic groups and scales. Overall, we found that the linear model (B) usually trended for LRS to increase with scale but only terrestrial plants were significant and terrestrial birds were borderline significant. In the quadratic model (D) when both spatial scale and study type (survey vs. list) were included in a multiple regression model, the study type was never close to significant, arguing that study type was not causing artefacts and that the differences could be attributed to scale (although spatial and temporal scale remain correlated). The datasets with fewer data points did not show a significant quadratic term, as might be expected given the power to detect such patterns decreases with data availability. The GLS model (E)

was similar but the quadratic term in terrestrial plants was no longer significant and freshwater fish became significant. The best variance model (homoscedasticity of OLS or exponential heteroscedasticity of GLS) varied widely between data sets, and in most cases, the difference in fit between the two was small. We interpret this and an examination of the visual plots as indicating neither OLS nor exponential GLS is a strong model of variance structure.

Table S2. Summary of statistical fits of different models for the cross-scale data.

	Data Statistics		Model A—Intercept Only			Model B—Linear OLS			
						Intercept		Slope vs. scale	
	# Obs.	% Survey	Mean	Std Dev.	p	Coef	p	Coef	p
Terrestrial Plants	818	58.1%	0.073	0.309	<0.0001	0.0908	<0.0001	0.0049	0.0894
Terrestrial Birds	288	3.1%	0.073	0.222	<0.0001	0.0491	0.0394	0.0246	0.0025
Terrestrial Mammals	173	6.4%	0.129	0.469	0.0004	0.0859	0.4386	-0.0233	0.6419
Marine Invertebrates	134	99.3%	0.098	0.497	0.0237	-0.2942	0.1624	-0.0637	0.0597
Marine Fish	101	98.0%	0.028	0.435	0.5243	0.0924	0.5073	0.0125	0.7434

Terrestrial Invertebrates	69	8.7%	-0.016	0.327	0.6795	-0.0959	0.1964	0.0075	0.6719
Freshwater Fish	49	4.1%	0.167	0.120	<0.0001	-0.0404	0.5954	0.0428	0.0095
Marine Plants	19	-	-	-	-	-	-	-	

1 Table S2. Continued

	Model D—Quadratic OLS					
	Slope vs. Scale		$Scale^2$		Study Type	
	Coef.	p	Coef	p	Coef	p
Terrestrial Plants	0.0143	0.0571	-0.0028	0.0072	0.0500	0.4411
Terrestrial Birds	0.0236	0.0064	-0.0125	0.0019	-0.0256	0.7634
Terrestrial Mammals	-0.0202	0.7101	0.0049	0.7745	-0.0228	0.8865
Marine Invertebrates	-0.0392	0.2539	-0.0094	0.5122	-0.2951	0.6101

Marine Fish	0.0015	0.9664	-0.0151	0.1144	-0.4215	0.2708
Terrestrial Invertebrates	-0.0006	0.9724	0.0047	0.5693	0.1434	0.4883
Freshwater Fish	0.0428	0.0418	0.0053	0.0816	-0.0927	0.4101
Marine Plants	-	-	-	-	-	

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3 Table S2. Continued

	Model E—Quadratic Variance GLS			
	Slope vs. Scale		$Scale^2$	
	Coef.	p	Coef	p
Terrestrial Plants	0.0049	0.0894	-0.0006	0.4161
Terrestrial Birds	0.0246	0.0025	-0.0133	0.0003

Terrestrial Mammals	-0.0233	0.6419	0.0058	0.7140
Marine Invertebrates	-0.0637	0.0597	0.0056	0.5370
Marine Fish	0.0125	0.7434	-0.0116	0.1346
Terrestrial Invertebrates	0.0075	0.6719	0.0039	0.4518
Freshwater Fish	0.0438	0.0095	0.0045	0.0240
Marine Plants	-	-	-	-

1 Table S2. Continued

	Model AIC Scores (Model C Vs. E)	
Terrestrial Plants	391.4532	137.7995
Terrestrial Birds	-63.7176	-62.2645
Terrestrial Mammals	235.3891	237.3873

Marine Invertebrates	196.6703	192.5339
Marine Fish	123.6297	122.4970
Terrestrial Invertebrates	45.5948	-71.9930
Freshwater Fish	-66.6704	-66.5679
Marine Plants	-	-

Table S2 – Statistical results of different models on different taxa groups. Taxa are sorted by the number of time-series available (column TS). %Survey indicates what fraction of the time-series were from surveys (e.g., BioTIME data) with the remainder being checklist type of data. Model A shows the mean LSR and a p-value for whether this mean is statistically significant from zero. Model B is linear and the slope coefficient and p-value for a test of a slope different from zero are shown. AIC scores compares model C (OLS quadratic) with model E (GLS quadratic) to see what error model fits best. Model D shows the coefficient (slope) and p-value for the linear, quadratic and study-type variables. A significant linear model indicates scale-dependence. A significant quadratic model indicates non-linear scale-dependence. Model E shows the slope and quadratic terms.

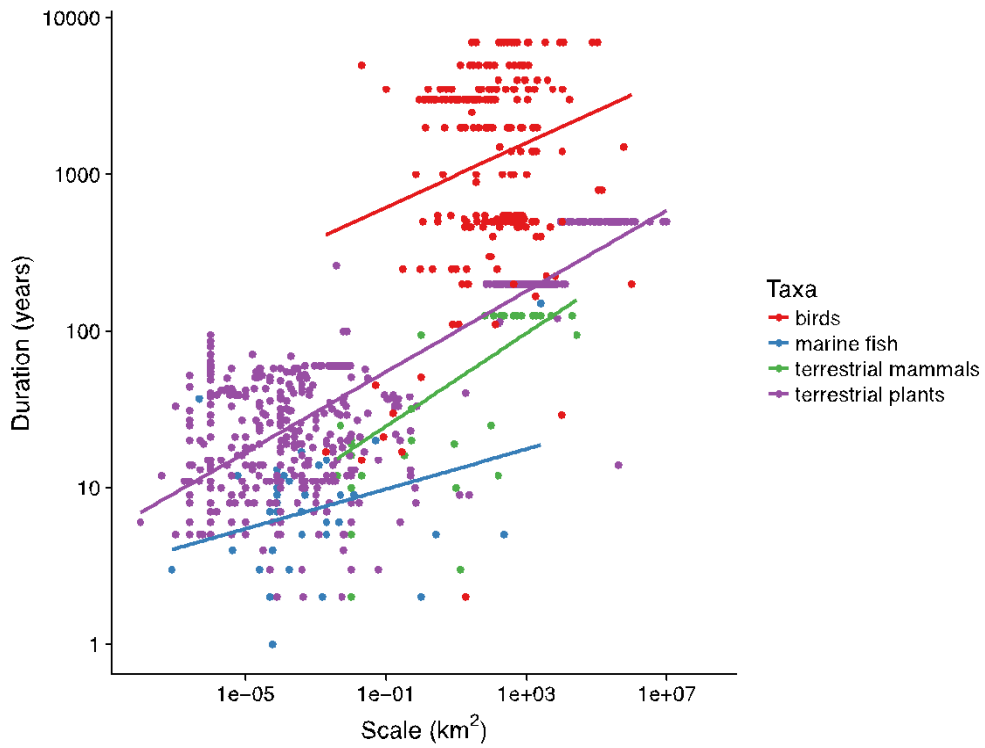

Figure S1. Illustration of the potential for covariance between the spatial scale of the study and the temporal duration of the study. Our main goal with this figure is simply to show that while the patterns from this analysis help us to understand that different perspectives on species richness change, the complexity of error structures and co-variance in the data suggest that any inferential statistics are cautionary.